

CHOLLA MORTALITY AND EXTREME DROUGHT IN THE SONORAN DESERT

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ABSTRACT

At the beginning of the 21st Century, deserts and woodlands of the southwestern United States were in the midst of a drought that contributed to massive die-offs for many plant species. In the northwestern Sonoran Desert, the drought contributed to extreme desiccation and mortality of cholla (*Cylindropuntia*) cacti. At low elevations (210–290 m), over half of the *Cylindropuntia bigelovii*, over 17% of the *C. echinocarpa*, 6% of the *C. ramosissima*, and less than 2% of the *C. ganderi* were dead by winter 2004/2005. At a higher elevation (~820 m), 26% of *C. bigelovii* and 14% of *C. ganderi* were dead by winter 2005/2006. The lower mortality for *C. bigelovii* at the higher elevation site was likely due to milder temperatures and greater precipitation; the greater mortality for *C. ganderi* at the same site may be the result of freezing or frost damage to tissues during the drought. Differences in mortality among species at both elevations were attributed to several factors, including: intra- and interspecific competition, reproductive strategy, and shoot architecture. Based on this study and previous research, it is believed that *C. bigelovii* experiences periodic extensive die-offs in response to extreme droughts, whereas populations of the other three species apparently change little during such droughts.

Key Words: Chollas, *Cylindropuntia*, desert, drought, mortality.

Populations of desert perennials are dynamic, with plant cover, mortality, and recruitment tied to several factors, especially total yearly or seasonal rainfall (Martin and Turner 1977; Goldberg and Turner 1986). Extreme climate events are believed to have a disproportionate effect on a variety of processes within organisms of a population (Gutschick and BassiriRad 2003). For populations of desert perennials to experience measurable changes, events such as drought must be prolonged or especially severe compared to the conditions they usually experience (Gutschick and BassiriRad 2003). Such a drought occurred throughout much of the southwestern United States around the turn of the 21st Century, with 2002 being the driest year on record for much of the region (NOAA, NCDC website, Breshears et al. 2005). Massive die-offs of many desert perennials occurred as a result of this drought (Miriti et al. 2007; McAuliffe and Hamerlynck 2010), as well as *Pinus edulis* Engelm. (Breshears et al. 2005). There is evidence that, in addition to low precipitation, increasing ambient temperatures (Breshears et al. 2005), differences in soil composition (McAuliffe and Hamerlynck 2010), and plant age (Miriti et al. 2007) affected mortality during this drought. Measured increases in minimum winter temperatures, as well as predicted increases in annual mean temperatures and a predicted drying of the entire region, indicate that droughts in the Desert

Southwest will likely increase in frequency and be more extreme in the future (Weiss and Overpeck 2005; Seager et al. 2007).

Desert cacti, especially barrel and columnar forms, are able to survive long-term drought because they have voluminous amounts of water-storage tissues (Gibson and Nobel 1986). They also tolerate some of the highest tissue temperatures of any group of vascular plants and can acclimate to higher temperatures than they typically experience (Smith et al. 1984). For cacti, the relative tolerance to high temperatures and drought is linked with morphology. Chollas (genus *Cylindropuntia* [Engelm.] F.M. Knuth of North America) have stems with relatively small volumes of water-storage tissues and high surface area to volume ratios (Gibson and Nobel 1986), characteristics that can lead to lower relative tissue temperatures in the field (Nobel 2009), which may be one reason why this growth form is successful in warm deserts of North America. However, because chollas likely experience lower stem tissue temperatures in the field, they have lower maximum viable tissue temperatures than barrel and columnar cacti (Smith et al. 1984). Thus, during extreme long-term drought with elevated temperatures, such as that experienced in the drought at the turn of the century (Breshears et al. 2005) and those predicted for the future (IPCC 2007), chollas may experience greater mortality than barrel and columnar cacti not

only because they store less water than these growth forms, but because their tissues may not be able to tolerate increases in temperature.

The severe drought at the end of the 20th and the beginning of the 21st centuries appeared to lead to extensive mortality for several cholla species in the northwestern Sonoran Desert. In early fall 2004, nearly every *Cylindropuntia bigelovii* (Engelm.) F. M. Knuth, *Cylindropuntia echinocarpa* (Engelm. & J. M. Bigelow) F. M. Knuth, *Cylindropuntia ganderi* (C. B. Wolf) Rebman & Pinkava, and *Cylindropuntia ramosissima* (Engelm.) F. M. Knuth at low elevations were extremely desiccated or dead and most living plants had not flowered or produced new stems for two years (M. Fisher personal communication). In the 1960's, *C. bigelovii* experienced a die-off at the same location (McDonough 1965).

For the recent drought, *C. bigelovii* clearly experienced extensive mortality. Mortality for the other species was difficult to assess initially because cacti can experience extreme desiccation and survive (Gibson and Nobel 1986). Thus, the purpose of the study was to determine how the morphology of each species and the apparent competition they experience were related to their relative mortality as a result of the drought. Because of the length and severity of the drought, it was hypothesized that species survival should depend on the ability to store water, which is related to stem volume and the amount of water storage tissue in the stems (Nobel 2009). Based on these criteria and previous research on the four species in Deep Canyon (Bobich and Nobel 2001), *C. ramosissima* should have experienced the greatest percent mortality, because its stems had the smallest volume and smallest amount of water storage tissue, followed in order by *C. echinocarpa*, *C. bigelovii*, and *C. ganderi*. It was also hypothesized that shorter species with more basal branches should have experienced lower mortality because they would experience lower water stress due to gravity and be able to sacrifice some of their canopy and survive, compared with taller species with fewer basal branches. In addition, species that experience the greatest competition for resources should experience the highest mortality. The effects of elevation on plant mortality were also assessed by observing *C. bigelovii* and *C. ganderi* at a higher elevation where they were hypothesized to have experienced lower mortality, because temperature decreases and rainfall increases as elevation increases. To test these hypotheses, morphological measurements, distances to nearest neighbors, and descriptions of patterns of shoot death were recorded. In addition, climate data were analyzed to compare the conditions prior to this study and those leading up to the previously reported die-off at the same site (McDonough

1965), and to compare the climate at the two sites in this study.

METHODS

Field Observations

Research was performed in the flood plain (210–290 m; 33°39'N, 116°22'W) and at Agave Hill (820 m; 33°38'N, 116°24'W) within the University of California, Riverside Philip L. Boyd Deep Canyon Desert Research Center (Deep Canyon) in Palm Desert, California. The following cholla species were studied in the flood plain: *Cylindropuntia bigelovii*, *C. echinocarpa*, *C. ganderi*, and *C. ramosissima*. Only *C. bigelovii* and *C. ganderi* occurred at Agave Hill. In the flood plain, 10 plants occurring approximately 238–250 m in elevation were not included in the study because they could not be positively identified to species.

At both sites, chollas were sampled in 10 m × 10 m quadrats. In the flood plain, four quadrats were placed roughly west to east every 0.2 km along a total distance of 2.8 km south from the fence at the north boundary of the Research Center. At Agave Hill, three quadrats were positioned roughly west to east on two north- and two south-facing slopes, for a total of 12 quadrats. Only chollas whose bases were in the quadrat boundaries were sampled. Dead chollas were included in the study if they possessed an intact epidermis over approximately 75% of their shoots, which would indicate that they died during the drought. Chollas in the flood plain were determined to be living or dead during the winter and early spring of 2004/2005 because the site received 269 mm of rain from October 2004 through February 2005 (average precipitation from July 1–June 30 for the site was 140 mm), allowing living plants to rehydrate and produce both new shoots and flowers. Chollas were studied at Agave Hill during winter 2005/2006 when all living plants possessed turgid shoots.

The following morphological measurements were recorded for individual plants: height, lengths of the major and minor axes of the canopy, and number of basal branches, which were defined as major branches originating within 0.2 m of the plant base. Height measurements for some of the dead *C. bigelovii* were approximated by measuring the height of the upright portion of the shoot and the length of the nodding or detached upper portion of the shoot lying near the base of the plant. Canopy spread was calculated by taking the square root of the product of the major and minor axes. Canopy axes were not measured for dead *C. bigelovii* because the majority of the lateral branches had detached; the dead individuals of the other three species appeared to have retained most of their

stems, allowing for canopy measurements. Observations of shoot death, including detached dead shoots, retained dead shoots, and the apparent direction of the death of the shoot (acropetal or basipetal), were made in an effort to relate morphology to mortality. Distance to the nearest cholla was recorded because chollas demonstrate a high-level of intraspecific and interspecific competition (Cody 1986a, b). Distance to the nearest shrub was also recorded because most of the shrubs at each site, represented primarily by *Ambrosia dumosa* (A. Gray) W.W. Payne, *Encelia farinosa* A. Gray ex Torr., and *Larrea tridentata* (Sessé & Moc. ex DC.) Coville in the flood plain and *Ambrosia dumosa*, *Bahiopsis parishii* (Greene) E.E. Schill. & Panero, *Bebbia juncea* (Benth.) Greene, *Encelia farinosa*, *Eriogonum fasciculatum* Benth., and *Larrea tridentata* at Agave Hill, likely had a significant portion of their roots within the rooting zone of the chollas (Cody 1986b; Rundel and Nobel 1991; Nobel 1997; E. Bobich personal observations).

Climate Data

Precipitation and mean yearly temperature in Palm Springs were determined for the 10 seasons (July 1–June 30; 1954/1955–1963/1964) prior to the publication of the die-off of *C. bigelovii* in the early 1960's (McDonough 1965) and for the 10 seasons (1994/1995–2003/2004) leading up to this study. Climate data for Palm Springs were downloaded from the Desert Research Institute's Western Regional Climate Center website (wrrc.dri.edu). Because climate data for Agave Hill was not recorded until 1973, precipitation and mean yearly temperature for seasons 1973/1974–2003/2004 and the 10 seasons leading up to the drought (1994/1995–2003/2004) were compared between the flood plain and Agave Hill. In addition, the number of days with low temperatures $\leq 0^{\circ}\text{C}$ and days with low temperatures $0\text{--}2^{\circ}\text{C}$, which can lead to radiation frost or frost pockets and freezing damage to cacti, were recorded for the 10 seasons leading up to the drought for both the flood plain and Agave Hill.

Data Analysis

There were typically few individuals of each species in each quadrat, so the data for each species was pooled for both the flood plain and Agave Hill. Percent mortality was calculated for each species at both sites. Morphological data and distances to the nearest cholla and nearest shrub were not distributed normally for any of the species and the variances among species were rarely equal. Because most of the data could not be transformed to allow for parametric comparisons, comparisons of morphological data and

distances to the nearest cholla and nearest shrub among the species in the flood plain were performed using Kruskal-Wallis one way ANOVA. Comparisons between *C. bigelovii* and *C. ganderi* at Agave Hill were performed using Mann-Whitney U tests. Comparisons for *C. bigelovii* and *C. ganderi* between the flood plain and Agave Hill and between living and dead plants for each species within each site were also performed using Mann-Whitney U tests. For *C. ganderi* in the flood plain, living and dead individuals could not be compared because only one had died. Climate data for Palm Springs were compared between the 1954/1955–1963/1964 and 1994/1995–2003/2004 seasons using Student's t-test. Precipitation and temperature were compared between the flood plain and Agave Hill using paired t-tests, with data grouped by year. Data are presented as means $\pm 1\text{SE}$.

RESULTS

Distribution, Die-back, and Mortality of Chollas

Each cholla species in the flood plain had a different elevational distribution. The only species that occurred throughout the entire flood plain was *Cylindropuntia ramosissima*. *Cylindropuntia echinocarpa* had the lowest elevational range and was not sampled in quadrats above 244 m. The lowest elevation at which *C. bigelovii* and *C. ganderi* were sampled in the flood plain was 250 m, with *C. ganderi* apparently replacing *C. echinocarpa*; *C. bigelovii* was especially common on rockier soil. At Agave Hill (~ 820 m), *C. bigelovii* was sampled only on south-facing slopes, which is where they primarily occurred, whereas *C. ganderi* occurred in quadrats on both north- and south-facing slopes.

In late fall 2004, chollas in the Deep Canyon flood plain were extremely dehydrated and most had experienced substantial die-back, although the patterns of shoot die-back differed among species (Fig. 1). Most of the dead *C. bigelovii* had blackened shoots with black spines; living stems were usually bright green with yellow spines (Figs. 1A and 2). The shoots of *C. bigelovii* appeared to have died acropetally, the evidence being that living plants, as well as some of those that had collapsed, retained living stems on approximately the top or distal third of their shoots (Fig. 2). The shoots of many dead or dying *C. bigelovii* failed near the base and fell over or appeared to have collapsed (Fig. 2), but most plants that died had either a nodding shoot, with approximately the top third of the shoot bent downward, or the top third or quarter of the shoot had completely detached from the rest of the plant (Fig. 1A). For *C. echinocarpa* (Fig. 1B), dead stems occurred throughout the shoot canopy; in some cases, entire major branches



FIG. 1. Representatives of A) *Cylindropuntia bigelovii*, B) *C. echinocarpa*, C) *C. ganderi*, and D) *C. ramosissima* during the fall of 2004 in the flood plain of the Philip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA. Arrows indicate nodding shoots in A) and dead branches in B), C), and D).

had died. There were almost always dead small stems near the base of each *C. echinocarpa*. *Cylindropuntia ganderi* and *C. ramosissima* clearly experienced basipetal dieback, which often resulted in the death of entire major branches (Fig. 1C, D); however, whereas the dead terminal stems of *C. ganderi* were almost always attached to the plant, copious numbers of dead stems occurred at the base of all but the smallest *C. ramosissima*. The shoots of many of the largest *C. ramosissima* apparently split at the base, appearing initially as separate plants, especially those individuals whose bases were buried in mounds of sandy alluvium. After the rainfall in the winter of 2004/2005, many plants that initially appeared to have been dead, especially certain *C. ramosissima*, rehydrated and developed new stems.

The cholla species that experienced the highest mortality at both sites in the Boyd Reserve was *C. bigelovii* (Table 1). Over half of the sampled *C. bigelovii* were dead in the floodplain, whereas just over one-fourth were dead at Agave Hill (Table 1). Of the other three species that occurred in the flood plain, only *C. echinocarpa* experienced

over 10% mortality (Table 1). For *C. ganderi* in the flood plain, only one sampled individual had died, whereas 14% died at Agave Hill (Table 1). Almost 6% of the sampled *C. ramosissima* were dead in the flood plain by the spring of 2005 (Table 1).

Morphology and Proximity to Other Chollas and Shrubs

In the flood plain, *C. ganderi* was on average 75% as tall as the other three cholla species, but at Agave Hill it was statistically the same height as *C. bigelovii* (Table 2). *Cylindropuntia bigelovii* had the smallest canopy spread of the four species, with a canopy 40% as broad as those of *C. echinocarpa* and *C. ganderi*, and 24% of that of *C. ramosissima* in the flood plain. At Agave Hill, the spread of *C. bigelovii* was less than 50% of that of *C. ganderi* (Table 2). *Cylindropuntia bigelovii* also had the fewest basal branches, with almost all plants having a single trunk at both sites. In the flood plain, *C. ramosissima* had the most basal branches, followed in order by *C.*



FIG. 2. A) Two healthy and two collapsed dying individuals of *Cylindropuntia bigelovii* and B) a view of the collapsed dying individuals showing dead bases, leading to the collapse, and living stems on the apices of the shoots. The plants were located in the flood plain of the Philip L. Boyd Deep Canyon Desert Research Center, Palm Desert, CA.

ganderi and *C. echinocarpa* (Table 2). At Agave Hill, *C. ganderi* had three times as many basal branches as did *C. bigelovii* (Table 2).

In general, chollas were smaller at Agave Hill than in the flood plain. The heights of *C. bigelovii* and *C. ganderi* at Agave Hill averaged 71% of those in the flood plain (Table 2). Canopy spread and the number of basal branches did not differ between *C. bigelovii* in the flood plain and those at Agave Hill. For *C. ganderi* at Agave Hill, canopy spread was 75% smaller and individuals averaged one less basal branch than did those in the flood plain (Table 2).

In the flood plain, *C. bigelovii* individuals were nearly 1.0 m closer to other chollas, usually other *C. bigelovii*, than were plants of the other three species, all of which were similar distances from other chollas (Table 2). At Agave Hill, *C. bigelovii* was 0.7 m closer to other chollas than was *C. ganderi* (Table 2). *Cylindropuntia bigelovii* individuals were also 1.0 m closer to shrubs than were the other three species in the flood plain, whereas at Agave Hill *C. bigelovii* and *C. ganderi* were similar distances from the nearest shrubs (Table 2). Overall, chollas at Agave Hill were much closer to their nearest neighboring chollas and shrubs than were similar species in the flood plain (Table 2).

Dead individuals did not differ significantly from living individuals for any of the species in the flood plain or at Agave Hill in terms of

morphology (height, spread, and number of basal branches), or proximity to other chollas or shrubs (Table 2). At Agave Hill, dead *C. ganderi* nearly differed in height from living individuals; however, no other comparisons yielded $P < 0.12$ (Table 2).

Climate

For Palm Springs, the average precipitation for the 10 seasons (July 1–June 30) prior to the publication of McDonough (1965) was statistically the same as it was for the 10 seasons leading up to this study (Table 3), whereas the average yearly temperature for the 10 seasons leading up to this study was almost two degrees higher than it was from 1954/55–1963/64 (Table 3). From 1973/74 to 2003/04, the climate in the flood plain was warmer and drier than that of Agave Hill (Table 4). In fact, for every season, except 1986/87 and 1989/90, Agave Hill received more precipitation than did the flood plain, with the average seasonal precipitation in the flood plain 80% of that at Agave Hill. During that same period, the average daily temperature in the flood plain was over 3°C greater than that at Agave Hill (Table 4). Over the ten seasons leading up to this study, the flood plain again received approximately 80% of the precipitation at Agave Hill. During the same period, both the flood plain and Agave Hill received an average of 69% of the

TABLE 1. PERCENT MORTALITY FOR *CYLINDROPUNTIA BIGELOVII*, *C. ECHINOCARPA*, *C. GANDERI*, AND *C. RAMOSISSIMA* IN THE FLOOD PLAIN AND AT AGAVE HILL IN THE PHILIP L. BOYD DEEP CANYON DESERT RESEARCH CENTER, PALM DESERT, CA. Values in parentheses indicate the total number of individuals sampled at each location.

	<i>C. bigelovii</i>	<i>C. echinocarpa</i>	<i>C. ganderi</i>	<i>C. ramosissima</i>
Flood plain	55.6 (275)	17.5 (63)	1.6 (61)	5.9 (85)
Agave Hill	25.8 (128)	—	14.0 (57)	—

TABLE 2. MORPHOLOGICAL CHARACTERISTICS, DISTANCE TO THE NEAREST CHOLLA, AND DISTANCE TO THE NEAREST SHRUB FOR ALL OF THE SAMPLED INDIVIDUALS, AND THE LIVING AND THE DEAD INDIVIDUALS OF *CYLINDROPUNTIA BIGELOVII*, *C. ECHINOCARPA*, *C. GANDERI*, AND *C. RAMOSISSIMA* IN THE FLOOD PLAIN AND OF *C. BIGELOVII* AND *C. GANDERI* AT AGAVE HILL IN THE PHILIP L. BOYD DEEP CANYON DESERT RESEARCH CENTER, PALM DESERT, CA. For all of the sampled individuals, the first lowercase letter next to values refers to pairwise comparisons after Kruskal-Wallis ANOVA among the four species in the flood plain and Mann-Whitney U tests for comparisons between the two species at Agave Hill. The second lowercase letter next to the values of *C. bigelovii* and *C. ganderi* refers to Mann-Whitney U tests for comparisons between individuals in the flood plain and Agave Hill. Different uppercase letters denote differences between living and dead individuals within each species after Mann-Whitney U tests. Because dead *C. bigelovii* lost most of their canopy prior to the study, no comparisons for canopy spread were performed between living and dead individuals of that species. Data are means \pm 1SE. Note: only one dead *C. ganderi* was sampled in the flood plain.

		Height (m)	Canopy spread (m)	Number of basal branches	Distance to nearest cholla (m)	Distance to nearest shrub (m)
Flood Plain	<i>C. bigelovii</i>	All	0.62 \pm 0.02aa	1.1 \pm 0.0aa	1.79 \pm 0.09aa	1.35 \pm 0.08aa
		Living	0.59 \pm 0.03A	1.1 \pm 0.0A	1.87 \pm 0.14A	1.43 \pm 0.11A
	<i>C. echinocarpa</i>	Dead	—	1.1 \pm 0.0A	1.56 \pm 0.12A	1.26 \pm 0.12A
		All	0.69 \pm 0.05b	2.5 \pm 0.2b	2.83 \pm 0.27b	3.60 \pm 0.28b
	<i>C. ganderi</i>	Living	0.66 \pm 0.05A	2.5 \pm 0.2A	2.86 \pm 0.31A	3.58 \pm 0.29A
		Dead	0.81 \pm 0.13A	2.2 \pm 0.3A	2.62 \pm 0.27A	3.68 \pm 0.85A
Agave Hill	<i>C. bigelovii</i>	All	0.68 \pm 0.05ba	4.4 \pm 0.3ca	2.70 \pm 0.20ba	2.54 \pm 0.20ba
		Living	0.68 \pm 0.05	4.4 \pm 0.3	2.72 \pm 0.21	2.58 \pm 0.20
	<i>C. ramosissima</i>	Dead	0.47	3	1.9	0.38
		All	1.15 \pm 0.07b	5.1 \pm 0.4c	2.58 \pm 0.20b	3.69 \pm 0.30b
	<i>C. bigelovii</i>	Living	1.17 \pm 0.07A	5.2 \pm 0.5A	2.57 \pm 0.20A	3.69 \pm 0.31A
		Dead	0.83 \pm 0.14A	3.7 \pm 0.9A	2.70 \pm 1.36A	3.77 \pm 0.22A
	<i>C. ganderi</i>	All	0.24 \pm 0.01aa	1.1 \pm 0.0aa	0.54 \pm 0.04ab	0.55 \pm 0.03ab
		Living	—	1.1 \pm 0.2A	0.54 \pm 0.05A	0.57 \pm 0.04A
	<i>C. ganderi</i>	Dead	—	1.1 \pm 0.4A	0.53 \pm 0.08A	0.50 \pm 0.06A
		All	0.51 \pm 0.05bb	3.1 \pm 0.3bb	1.23 \pm 0.17bb	0.52 \pm 0.07ab
	<i>C. ganderi</i>	Living	0.52 \pm 0.06A	3.0 \pm 0.4A	1.23 \pm 0.19A	0.51 \pm 0.07A
		Dead	0.34 \pm 0.07A	4.0 \pm 0.8A	1.16 \pm 0.16A	0.57 \pm 0.09A

TABLE 3. MEAN PRECIPITATION AND TEMPERATURE FOR PALM SPRINGS FOR THE 1954/1955–1963/1964 SEASONS AND THE 1994/1995–2003/2004 RAINFALL SEASONS. Temperatures were not included for 1958/59 and 1963/64 due to insufficient data. Values with different letters within a row indicate a significant difference ($P < 0.05$) for Student's t-test. Data are means \pm 1SE.

	1954/1955–1963/1964	1994/1995–2003/2004
Precipitation (mm)	95.0 \pm 14.6a	85.0 \pm 22.4a
Temperature (°C)	22.1 \pm 0.2a	24.0 \pm 0.3b

average seasonal rainfall they received from 1973/1974 to 2003/2004 (Table 4). The two seasons with the lowest precipitation at both sites were 1998/1999, with 49.3 mm received in the flood plain and 68.8 mm at Agave Hill, and 2001/2002, with 57.4 mm received in the flood plain and 67.4 mm at Agave Hill; the calendar year with the lowest precipitation was 2002, with the flood plain receiving 26.9 mm and Agave Hill 37.8 mm. The average temperature for the 10 seasons leading up to this study was over 4°C greater in the flood plain than at Agave Hill (Table 4).

The low temperatures in the flood plain were never $\leq 2^{\circ}\text{C}$ during the 10 seasons prior to the study. At Agave Hill, there were three freezing days, occurring in December 1998 (0.0°C), April 1999 (0.0°C), and January 2002 (-0.5°C). Each freezing day was preceded by and/or followed by days with low temperatures $0\text{--}2^{\circ}\text{C}$. Overall, there were 23 d with low temperatures $0\text{--}2^{\circ}\text{C}$ at Agave Hill, with all of them occurring during the 1997/98–2001/02 and 2003–2004 seasons.

DISCUSSION

The cholla species that experienced the greatest mortality in Deep Canyon during the most recent drought was *C. bigelovii*, with populations decreasing over 50% in the flood plain and over 25% at Agave Hill. McDonough (1965) reported that *C. bigelovii* experienced greater than 50% mortality in Deep Canyon approximately 40 yr earlier, but did not attribute the mortality to any one factor. Populations of *C. bigelovii* may be stable for several decades and individual plants can live over 60 yr (Hastings and Turner 1965). Based on the results of this study and McDonough (1965), and the climate leading up to both studies, it can be assumed that, at least in the northwestern Sonoran Desert, the populations of *C. bigelovii* are dynamic and experience

repeated die-offs that likely result from extreme drought.

The greater susceptibility of *C. bigelovii* to drought compared with the other cholla species is related to its morphology, reproductive mode, and low genetic diversity. The shoots of *C. bigelovii* almost always had one basal branch (trunk), which is typical for the species (McDonough 1965; Turner et al. 1995). Thus, if the trunk fails, that individual essentially dies. Unlike the other three species, all of which depend on sexual reproduction to regenerate populations, *C. bigelovii* rarely produces viable seeds (Pinkava et al. 1985) and almost solely propagates vegetatively via the successful rooting of detached stems (Benson 1982; Nobel et al. 1986; Bobich and Nobel 2001). Thus, *C. bigelovii* likely experiences acropetal shoot death to allow individuals to keep their young stems, which are their propagules, alive to regenerate their populations. For the other three species that depend on sexual reproduction, survival of adults is important because successful seedling recruitment of cacti in deserts is rare (Gibson and Nobel 1986). Finally, *C. bigelovii* appears to be sterile and completely dependent on vegetative reproduction because it is triploid (Pinkava and Parfitt 1982; Baldwin et al. 2012) throughout much of its range. As a result, the genetic diversity of *C. bigelovii* is likely very low, which could make certain clones especially susceptible to adverse conditions like extreme drought, resulting in relatively high mortality for this species.

Because *C. bigelovii* reproduces vegetatively and its propagules are large (Bobich and Nobel 2001), its populations tend to be aggregated (McDonough 1965), which should lead to increased intraspecific competition. *Cylindropuntia acanthocarpa*, *C. echinocarpa* and *C. ramosissima*, tend to be randomly or regularly spaced and avoid neighboring conspecifics and/or congeners

TABLE 4. MEAN PRECIPITATION AND TEMPERATURE FOR THE 1973/1974–2003/2004 AND 1994/1995–2003/2004 SEASONS IN THE FLOOD PLAIN AND AGAVE HILL IN THE PHILIP L. BOYD DEEP CANYON RESEARCH CENTER. Yearly rainfall and mean temperature were compared between sites using paired t-tests; values with different letters within a row indicate a significant difference ($P < 0.05$) between the sites. Data are means \pm 1SE.

	1973/1974–2003/2004		1994/1995–2003/2004	
	Flood plain	Agave hill	Flood plain	Agave hill
Precipitation (mm)	156 \pm 17a	193 \pm 20b	108 \pm 24a	134 \pm 26b
Temperature (°C)	23.8 \pm 0.2a	20.6 \pm 0.2b	24.5 \pm 0.3a	20.0 \pm 0.5b

(Cody 1986a, b). The aggregated distributions of *C. bigelovii* are likely to exist for long periods between extreme droughts, after which extensive mortality drives populations towards a more random distribution, as hypothesized by McDonough (1965). *Cylindropuntia bigelovii* were also closer to shrubs than the other cholla species in the flood plain, reflecting the fact that the species occurs in areas with relatively high plant ground cover (E. Bobich, unpublished results). Thus, interspecific competition may have also contributed to the relatively high mortality of this species in the flood plain.

The species with the lowest percent mortality in the flood plain was *C. ganderi*, which was also the shortest of the cholla species; *C. ganderi* also had a similar number of basal branches to those of the most prolifically branched species, *C. ramosissima*. Like *C. ramosissima*, *C. ganderi* experienced abscisic acid shoot death, reflecting the tendency for adults to persist because they likely reproduce solely from seed (Bobich and Nobel 2001). *Cylindropuntia ganderi* did appear to lose fewer stems during the drought than the other species in the study, which is likely because it has extremely fibrous wood in its terminal stem junctions, whereas the other three species completely lacked fibers in those regions (Bobich and Nobel 2001). The resistance of *C. ganderi* to mortality in the flood plain may be because it has the greatest stem capacitance based on stem volume of the four species studied (Bobich and Nobel 2001), and its stems are very tolerant of high temperatures (Nobel and Bobich 2002). The effect of how its relatively short height might have contributed to its high survivorship is unclear, because the difference in height between *C. ganderi* and the other cholla species would have a small effect on water potential, yet the relatively low stature and surface area/volume of its shoots could have resulted in it depleting less soil water than the other species in the flood plain.

Elevation affected mortality of *C. bigelovii* and *C. ganderi* differently. Typically, *C. ganderi* occurs at higher elevations than does *C. bigelovii* (Baldwin et al. 2012), which may be related to their relative abilities to establish in colder microclimates. In fact, at Agave Hill *C. bigelovii* occurs almost exclusively on south-facing slopes, which experience the highest local temperatures, whereas *C. ganderi* occurs on slopes of all aspects. At Agave Hill, mortality for *C. bigelovii* was half of what it was in the flood plain, supporting the hypothesis that the lower daily high temperatures and greater rainfall at Agave Hill should lead to reduced mortality; however, mortality of *C. ganderi* was over seven times greater at Agave Hill than in the flood plain. Although productivity appears to increase with increases in elevation for *C. ganderi*, the amount of tissue

damage for this species also increases with increasing elevation (Nobel and Bobich 2002). One reason for the increased tissue damage at higher elevations compared with lower elevations may be because *C. ganderi* stems are less tolerant of low than high temperatures, suffering 50% tissue death at -4.9°C and 69.5°C after temperature acclimation, respectively (Nobel and Bobich 2002); these values are -7.3°C (Nobel 1982) and 59.0°C (Didden-Zopf and Nobel 1982) for *C. bigelovii*, respectively (Nobel 1988). Furthermore, *C. ganderi* has a relatively open canopy that results in lower shoot temperatures than other cacti (Nobel et al. 1991) and has an apparent increased need for nurse plants at high elevations (Nobel and Bobich 2002), likely for protection from freezing temperatures; nurse plants would not have supplied much cover during the drought because of dieback and relative leaflessness. Considering that there were three freezing episodes at Agave Hill in the seven seasons prior to the study, with one being in January 2002, the driest year on record, it is possible that drought combined with susceptibility to freezing and frost damage led to greater mortality of *C. ganderi* at Agave Hill than in the flood plain.

In this study, *C. ramosissima* had the smallest stems in terms of mass and diameter (Bobich and Nobel 2001), making individual stems more susceptible to dehydration (Nobel 1988) than those of the other three species due to the lack of stem capacitance. Although there was a considerable amount of standing dead and detached dead stems near individuals, mortality was relatively low (6%) for *C. ramosissima*, which may be due to several factors, including the relatively high number of basal branches and the large canopy spread of the individuals. Different branches emanating from the bases of *C. ramosissima* appeared to respond to the drought differently, with some branches dying completely, while others survived and produced new stems and flowers after the winter of 2004/2005, indicating that this species experiences branch sacrifice during drought (Rood et al. 2000). The shoots of larger *C. ramosissima* appeared to split at the base, possibly allowing each resulting section to act independently of each other, as occurs for desert shrubs (Schenk 1999). Thus, individual *C. ramosissima* may increase their chances of long-term survival by compartmentalizing their shoots and stem redundancy. Of the four cholla species in this study, *C. ramosissima* was the only one that apparently experienced shoot splitting.

The low mortality of *C. ramosissima* in the flood plain of Deep Canyon is in contrast with the response of the species to the drought in Joshua Tree National Park, where over 50% of the adults died between 1999 and 2004 (Miriti et al. 2007). The difference in mortality of this

species between the sites may be related to the fact that the drought was especially severe in Joshua Tree National Park, resulting in massive die-offs of *A. dumosa* and other shrubs as well as the highest mortality observed for *L. tridentata* in the Mojave or Sonoran Deserts after the drought (McAuliffe and Hamerlynck 2010). Furthermore, the site where *C. ramosissima* was studied (1006 m) was near the elevational limit of the species (1100 m; Baldwin et al. 2012) and, as such, the individuals at that site could have been more susceptible to extreme changes in climate.

Cylindropuntia echinocarpa was the only species other than *C. bigelovii* to experience over 10% mortality in the flood plain. The stems of *C. echinocarpa* have a small capacitance compared to those of *C. bigelovii* and *C. ganderi* (Bobich and Nobel 2001), explaining why there were dead stems at the bases of individuals. *Cylindropuntia echinocarpa* had an intermediate canopy spread and number of basal branches compared to the other three species, meaning that although they might be able to compartmentalize their shoot mortality, the loss of one basal branch would result in a loss of 40% of their canopy compared to less than 25% for *C. ganderi* and *C. ramosissima*. Thus, it is likely that the intermediate mortality of *C. echinocarpa* during the drought is related to its morphology.

Dead individuals did not differ from living individuals in morphology or their proximity to other chollas or shrubs for any of the cholla species. Juvenile desert shrubs tend to experience greater mortality than adults and their mortality is not related to their relative distribution within a population (Wright and Howe 1987). Further, seedlings and young juvenile cacti are extremely susceptible to desiccation (Gibson and Nobel 1986). Miriti et al. (2007), who separated plants into juveniles and adults for perennials in Joshua Tree National Park, found that juvenile *C. ramosissima* experienced greater percent mortality than did adults between 1999 and 2004. Because the drought was prolonged and there was likely low recruitment during that period, it is probable that the cholla populations in Deep Canyon had few individuals younger than five-years-old at the time of this study. Thus, even if there was selection against younger individuals in Deep Canyon during the drought, it might not have been detectable in this study.

Most climate models for the Sonoran Desert indicate the region will be warmer and drier, with droughts being longer and more severe (Weiss and Overpeck 2005; Seager et al. 2007), which is somewhat supported by the 2°C increase in mean annual temperature in Palm Springs from the 1950's and 1960's to the most recent drought. Climate has already been cited as the main factor in the upward change in elevational ranges of some of the most prominent perennial plants in

the Deep Canyon drainage (Kelly and Goulden 2008). How these predicted changes in climate will affect cholla populations is unclear because mortality was low for the sexually reproducing species during this drought, which included the driest year on record, and because each species appears to have different adaptations to deal with prolonged drought. The sexually reproducing species, *C. echinocarpa*, *C. ganderi*, and *C. ramosissima*, may experience greater changes than *C. bigelovii* in elevational range over time because seedling recruitment should be lower in the predicted future climates, whereas *C. bigelovii* stems have a large capacitance and can produce roots readily when exposed to moist soil (Bobich and Nobel 2001). Thus, although *C. bigelovii* individuals clearly experienced the greatest mortality due to the most recent major drought compared with sexually reproducing species, it is not indicative of their relative future success in the northwestern Sonoran Desert.

CONCLUSIONS

Cholla species responses to the recent severe drought in the northwestern Sonoran Desert were related the primary mode of reproduction, which was related, in part, to their morphological characteristics, and proximity to other competing plants. Mortality was highest in the flood plain at Agave Hill for *C. bigelovii*, which is the only cholla species that relied completely on vegetative reproduction. Because their youngest stems are their propagules, *C. bigelovii* plants sacrificed their single trunk, essentially killing the individuals, to keep their youngest stems alive. *Cylindropuntia bigelovii* also experiences the greatest intraspecific competition of the four species because its reproductive mode leads to closer groupings of individuals. Individuals of the other three species appeared to sacrifice different parts of their shoots for plant survival. Young stems died throughout the canopy for *C. echinocarpa*, with plants rarely losing entire basal branches, whereas terminal stems and entire major branches died on *C. ganderi* and *C. ramosissima*, both of which had several major branches; *C. ganderi* retained its stems and responded as a single plant, whereas all *C. ramosissima* shed their youngest stems and the largest individuals responded to the drought as several independent units. Mortality for *C. bigelovii* was lower at Agave Hill, which is cooler and receives more rain than does the flood plain, whereas mortality for *C. ganderi* increased with increases in elevation, possibly reflecting a susceptibility to low temperature tissue damage during the extreme drought.

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